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THE LIFE CYCLE OF *PEACHIA QUINQUECAPITATA*, AN ANEMONE PARASITIC ON MEDUSAE DURING ITS LARVAL DEVELOPMENT

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Peachia quinquecapitata McMurrich (1913) is a burrowing anemone of the family Haloclavidae found on the Pacific coast of North America. McMurrich described the adult *P. quinquecapitata* and also indicated that a larval anemone parasitic on the hydromedusa *Aequorea* probably belonged to this same species. However, since he could not raise one to the adult, non-parasitic stage, he placed it in the genus *Bicidium*, created by Agassiz (1859) for a parasite of a scyphozoan medusa on the Atlantic coast of North America.

Nyholm (1949) discussed the possible dispersal mechanisms available to burrowing anemones such as *Halcampa* and *Peachia*. He cited reports in the literature concerning the development and parasitic habits of *Peachia* and concluded that members of this genus are not obligate parasites, but that eggs or larval anemones attaching to medusae by chance would provide for species dispersal. He noted the paucity of information on the life cycle of this genus, particularly concerning the initiation of parasitism and the nature of the parasitic relationship. The research reported here represents an attempt to provide this information.

Materials and Methods

This research was conducted during the summer of 1967 and the spring and summer of 1970 at the Friday Harbor Laboratories, Friday Harbor, Washington.

The free-living adult specimens of *P. quinquecapitata* were collected by digging in the low intertidal (–1.0 ft or lower) of sandy areas, or by dredging on sandy-mud bottoms. The adults were kept in 12 cm of sand in a sea water table filled to 20 cm with water. They were fed approximately once a week with pieces of shrimp meat or various polychaetes. A fluorescent lamp suspended above the tank provided about 120 foot-candles of light at the water's surface, and was set for 15 hours on and 9 hours off. Water flowing into the tank maintained the temperature at 12–15° C during the summer months.

To induce spawning, the anemones were first kept in the dark for 36–60 hours. After the dark period the tank was uncovered and the anemones returned to the normal light cycle. In addition to the fluorescent lamps, incandescent lamps were also turned on to give about 400 foot-candles at the water's surface. The water flow was stopped for 8 hours each day, increasing the temperature to about 15–18° C. The application of increased light and temperature was continued for a maximum of 15 days or until the anemones spawned.

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The eggs and sperm were collected as they were released. Fertilization and development were allowed to proceed in glass dishes. The sperm were rinsed from the eggs after one hour. The developing embryos were removed to fresh sea water after 12 hours. Subsequently the culture water was changed twice weekly.

Gametes and developing embryos were fixed at various stages for histological and cytological observations. Specimens to be embedded in paraffin were fixed either in Bouin's fluid or Sanfelice's fluid, then dehydrated in a graded series of ethanol and cleared in toluene prior to embedding. Material embedded in Epon was first fixed in 2% glutaraldehyde in Millonig's phosphate buffer (pH 7.4) with the osmolarity adjusted to 970 Milliosmoles. Following the one hour primary fixation the material was post-fixed in 1% Osmium tetroxide in the same buffer for one hour.

The host medusae, *Phialidium gregarium* (Hydrozoa, Campanulariidae), were collected with a dip net from the docks at Friday Harbor Laboratories and kept in jars containing 500 ml of sea water. The jars were partially immersed in a sea table maintaining a temperature of 12–14° C.

The medusae were infected by placing them individually into jars containing 10 to 20 planulae. Alternatively a single planula was pipetted into the stomach of the medusa. Every second day, each medusa and parasite was examined with a dissecting microscope. The parasite was measured and its development noted. To facilitate measurement a small amount of 20% magnesium sulfate was added to the examining dish. This quickly relaxed the medusa. Each medusa was checked for its general condition and the number of gonads remaining. Upon being returned to fresh sea water, the medusa began to swim within two minutes. If the host had little or no gonad tissue remaining, a fresh medusa of the same sex as the original host was put into the culture jar with the host and parasite. The medusae were fed plankton daily.

In 1967 the growth of the parasites was studied from naturally parasitized specimens of *Phialidium gregarium*. These medusae were collected from the docks with a dip net, returned to the laboratory and examined with a dissecting microscope. The medusae having parasites were placed in separate culture jars and checked every second day. In both 1967 and 1970 the rearing experiments were continued until the anemones dropped off the host and became free-living.

Results

Spawning

During the summer of 1967, adult specimens of *Peachia* were kept in the laboratory under normal laboratory light conditions. Attempts to induce spawning by temperature increase and electric shock were unsuccessful and none of these anemones spawned spontaneously. The method of inducing spawning described above was effective, but the time of gamete release varied from 4 to 360 hours after the end of the dark period.

The anemones spawned on 12 separate occasions between March and November 1970. Six of these spawns involved both males and females. Males were observed releasing sperm one-half to two hours before the females released eggs in

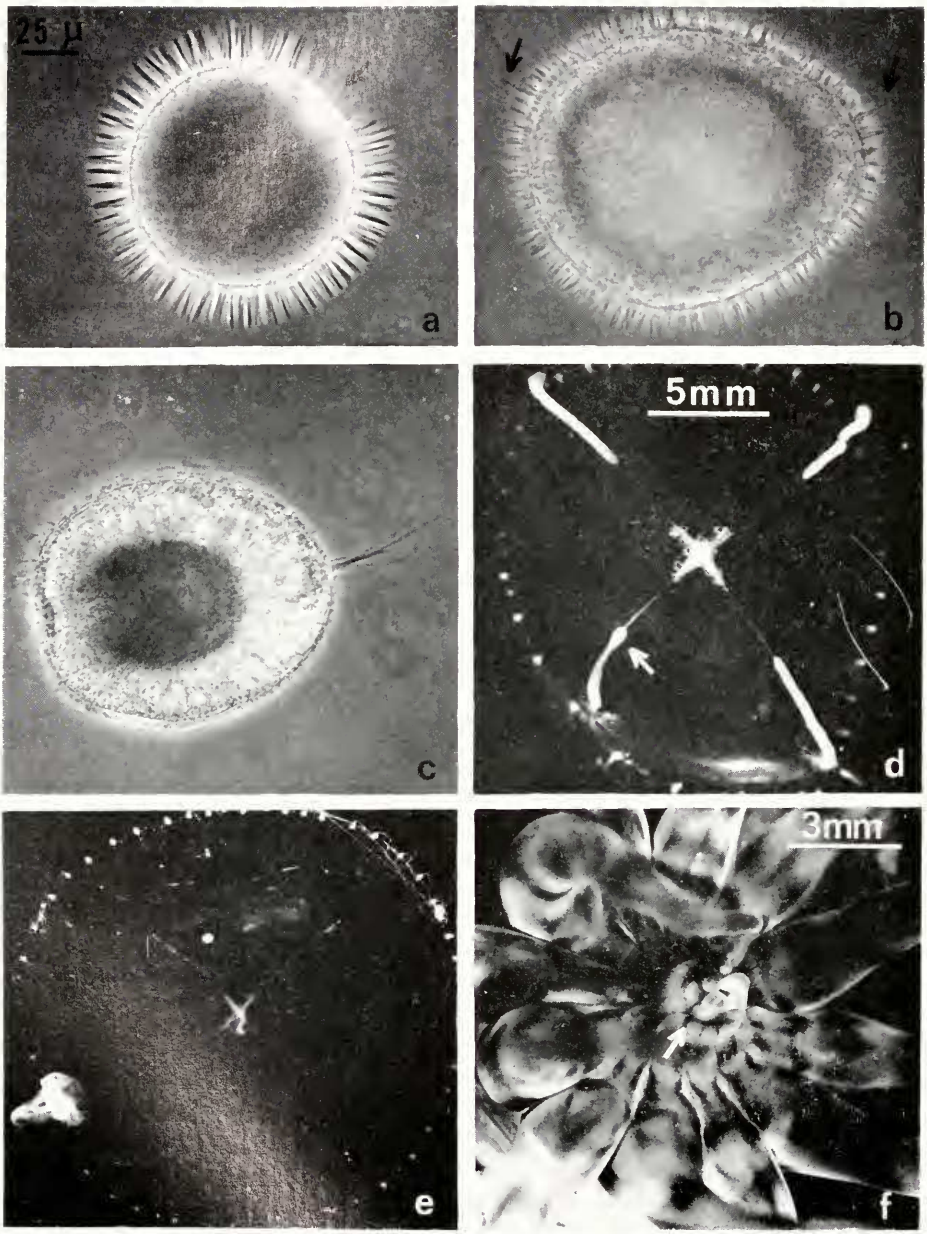

FIGURE 1. Developmental stages of *Peachia quinquecapitata;* (a) The unfertilized egg. The arrow indicates the egg nucleus and the part of the oolemma free of spines; (b) The late blastula stage, Cilia have developed (arrows) and the spines are reduced in length; (c) The planula stage with the characteristic apical tuft. The spines are now gone; (d) Young anemone at the late endoparasitic phase in the proximal part of the gonadal cavity (arrow); (e) later ectoparasite that has 12 tentacle buds; (f) Mature adult showing the details of the mouth (arrow) and conchula.

four of the cases. Two of the spawns were not observed until both sexes were releasing. Of the six spawns involving only one sex, four were by males.

During the time the gametes are being released by *P. quinquecapitata* the anemone pushes up out of its burrow one-third to one-half of its length. In still water the eggs settle close to the female and the mucus released with them rapidly dissipates. The sperm are also released with mucus, which sometimes forms a string before dissipating.

Gametes

The sperm measure 80 to 90 μ in length, the head being about 6.5 by 5.5 μ. The mid-piece is in the form of two swellings which probably contain the mitochondria.

The eggs are 110 μ to 120 μ in diameter and are covered with 20 μ spines, except in the region of the egg nucleus (Fig. 1a). Preliminary electron micro-

TABLE I

Timing of events during the early development of P. quinquecapitata; *water temperature in cultures, 14° C*

Time in hours	Event
0	Fertilization
2	1st cleavage
3	2nd cleavage
4	3rd cleavage
5	4th cleavage
6	5th cleavage
8	Becomes hollow blastula
10	Unfertilized eggs disintegrate
16	Cilia appear between the spines
20	Spines becoming shorter
28	Gastrulation starts
32	Spines no longer visible
40	Apical tuft forms

graphs indicate that they are extensions of the oolemma. There are no membranes external to the oolemma. The germinal vesicle is broken down to or at the time of spawning. Attempts to fertilize eggs removed from ripe gonads, but still possessing the germinal vesicles were unsuccessful.

Development to the planula

At 14° C cleavage begins about two hours after fertilization. Table I gives the timing for various events in development. The early cleavages sometimes appeared irregular at the four-, eight-, and sixteen-cell stages. The blastula is hollow, about 120 μ in diameter, with a lumen of 80 to 85 μ. During the blastula stage the pigment and yolk granules in the cells move to the basal end of the cells. The spines remain until late in the blastula stage. At about 16 hours cilia begin to appear between the bases of the spines (Fig. 1b). Their beating is uncoördinated until 4 to 8 hours have passed. At the time that the cilia begin to appear

the spines begin to shorten. Within 8 hours they are reduced in length to about 5 μ, continuing to shorten until they are no longer visible in the light microscope.

Gastrulation occurs by invagination beginning about 28 hours after fertilization. The gastrula is bullet-shaped and swims strongly. The planula stage is reached when the long apical cilia appear (Fig. 1c).

Planulae have been maintained in the laboratory for as long as 30 days in both filtered and non-filtered water. During this time no growth or development was observed. The planulae remained in good condition until about the 28th day when they began to move less vigorously. After 30 days, most were no longer moving and were disintegrating. While in good condition the planulae show a slight positive reaction to light.

Initiation of the parasitic relationship

Field collections of the host medusa, *Phialidium gregarium*, made in 1967 indicated that the smallest parasites were about 120 μ, hollow, had no septa and were located in the stomach or radial canals of the medusae. In addition to the parasites, the stomachs of the medusae contained a number of food items such as eggs and diatoms whose size was similar to that of the smallest parasites. The hypothesis suggested by these data is that the planula or some earlier developmental stage of the anemone is ingested by the medusa during normal feeding, thus initiating the parasitic phase of the anemone's life cycle.

Medusa were put in jars with planulae in 34 initiation trials. Initiation of the parasitic relationship was considered successful if the laral anemone was ingested and survived 24 hours in the gastrovascular cavity of the host. The medusae were examined at various times during the first 24 hour period. At the end of 24 hours planulae were present in 27 of the medusae. In a number of the trials the medusae were watched continuously. Within 10 to 30 minutes after being put into the jar the medusae began to show feeding behavior. Medusae examined after one-half to three hours had one to four planulae in their stomachs, those examined at the end of twelve hours had from one to ten planulae.

To test for possible host-directed swimming by the planulae, isolated stomach-manubrium preparations of *Phialidium* were placed in dishes with planulae. Twelve to twenty-four hours later the stomach contained one to three planulae. In one case a planula was observed as it contacted the oral folds. It remained motionless for a few moments and then was moved into the stomach by cilia of the manubrial epithelium. Isolated stomach-manubrium preparations were put into capillary tubes 5 mm long and with inside diameters of 1.1 or 1.2 mm. Identical empty capillary tubes of the same size were used as controls. In five trials there was no greater density of planulae in or around the capillary containing the medusa tissue.

The first attempts to rear these planulae as parasites in the laboratory after initiation were unsuccessful. The medusae were fed brine shrimp (*Artemia*) prior to and at the time the planulae were in the gastrovascular cavity. Thirty such attempts were made and none of the planulae survived beyond two days. Ten attempts were made with medusae that were starved after the planulae were introduced into the stomach. None of these planulae survived more than two days.

In all subsequent attempts the medusae were fed daily with plankton obtained with a no. 12 plankton net and consisting primarily of arthropods and algae. Under these feeding conditions, the planulae successfully parasitized the medusae. Single planulae were introduced into 65 medusae and of these, 30 lived longer than 2 days. Ten from this group of 30 successful starts completed the parasitic stage and became free-living.

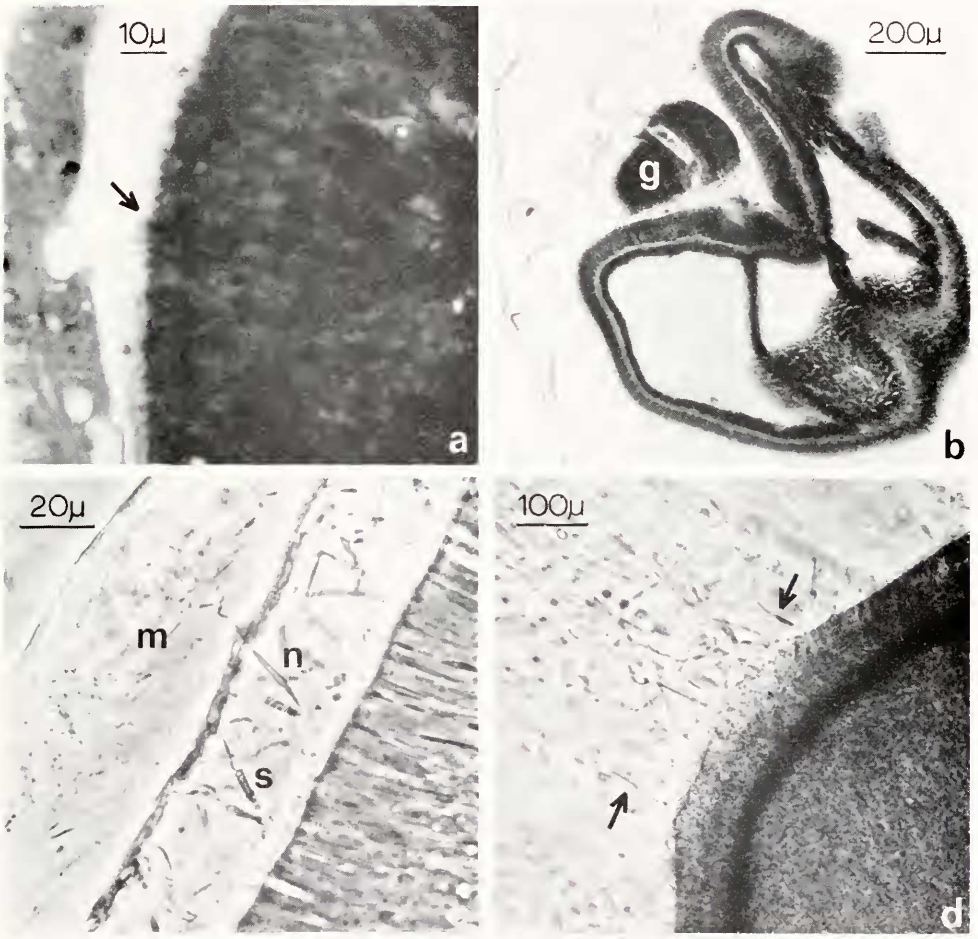

FIGURE 2. Additional details of the parasitism by *Peachia quinquecapitata*. (a) A section of an endoparasite in the radial canal of its host. The arrow indicates the blebbed epidermis of the anemone. Epon section stained with 1% aqueous p-phenylenediamine; (b) Longitudinal section of a parasite on the gonad (g) of the host medusa. Note that the shape of the gonad matches that of the mouth of the parasite. Paraffin section stained with hematoxylin and eosin; (c) Longitudinal section of the oral disk of an ectoparasite attached to the subumbrella of a medusa (m). A nematocyst (n) is shown penetrating the host tissue. Discharged spirocysts (s) are also present. Epon section stained with Azure II, Methylene Blue; (d) A phase contrast micrograph of a tentacle bud showing the discharged nematocysts (arrows) penetrating the subumbrella of the host medusa; a living preparation.

Endoparasitic phase

The planulae that survived in plankton-fed medusae began to show a noticeable increase in size by the second to fourth day. The developing larvae remained in the gastrovascular cavity of the host for an average of 11 days in the 1970 rearing experiments (Fig. 1d). They reached an average diameter of 0.5 mm before becoming ectoparasites. Figure 2a is a photomicrograph of a cross section of a parasite in the radial canal of a medusa. The epidermal cells are blebbed, indicating that they are probably obtaining food from the gastrovascular cavity of the host by phagocytosis. The larvae become ectoparasitic either by moving into the stomach and then out the mouth or by "burrowing" through the radial canal tissue.

Ectoparasitic phase

Once outside the host, the parasite moves to a gonad and begins to feed as shown in Figure 1e. A longitudinal section of a parasite on the partially eaten gonad of the host is shown in Figure 2b. Serial sections of this preparation showed complete and untouched gonads in one direction and completely grazed gonad in the other direction. The anemone attached to its host by means of nematocysts during the ectoparasitic phase. Figure 2c shows a cross section of the oral disk of a parasitic anemone with its nematocysts fired into the subumbrella of the host medusa. Figure 2d is a phase contrast micrograph of the tentacle bud of a living *Peachia* attached to its host. The discharged nematocysts are clearly visible.

As the parasites grow their shape changes from that of a flattened sphere to that of a cone with equal length and base diameter. As growth continues the anemone elongates more rapidly than its diameter increases (Fig. 1e). The first eight tentacle buds appear at approximately the 13th day. At this time the anemones averaged 1.5 mm in length and 1.22 mm in oral disk diameter. Four more appear within a short time, making a total of twelve tentacles. The parasites range from dull white to pink in coloration. The first sign of the adult color pattern is the appearance of the light and dark bands on the tentacles. This occurs on approximately the 26th day of the ectoparasitic phase.

The time when the siphonoglyph begins to develop is difficult to determine because the mouth and oral disk of the parasite are held against the host. The smallest anemone on which a siphonoglyph was seen was 0.5 by 0.5 mm. The siphonoglyph in this case was a wide shallow groove. As the parasite increases in size the groove becomes narrower and deeper. Eventually the areas where the siphonoglyph joins the pharynx come together forming the tube-like structure characteristic of the adult. While the anemone is on the host the mouth and part of the pharynx are pressed against the host. This tends to keep the edges of the siphonoglyph from coming together. When the parasite becomes free-living, the oral disc flattens, the pharynx is pulled in, and the edges of the siphonoglyph meet to form a tube.

Bordering the upper margin of the siphonoglyph are papillae which form the conchula (Fig. 1f). They are often not visible until the anemone becomes free-living. They appear first as three small swellings, two lateral and one ventral to

the siphonoglyph. Later two more swellings appear between the lateral and ventral papillae.

In the 1970 experiments, the anemones remained ectoparasite for an average of 31 days. During this time the adult characteristics developed, and they attained an average length of 4.19 mm and a diameter of 2.33 mm. At the end of the ectoparasitic phase the anemones generally released from their hosts, fell to the bottom, and burrowed into the sand if it was present. In a few cases the anemones remained on their hosts, feeding on them until nothing but an epithelial-covered bell remained and it sank to the bottom. The total parasitic stage lasted an average of 41 days in the 1970 experiment.

In 1967 the growth experiment was carried out using anemones obtained as naturally occurring parasites of *Phialadium gregarium*. These host medusae were put into culture before the parasite left the gastrovascular system of the host. In order to compare these data with those of 1970, the day on which the parasites moved from the gastrovascular cavity to the outside was arbitrarily designated as day 11, the average day for this event in 1970. Twenty parasites were reared in the laboratory in 1967. Thirteen of these anemones developed to the free-living stage, four were lost by accidents and three were still parasitic at the end of the time available for the experiment. A comparison of the 1967 and 1970 data was made using the *t* test. This showed no significant difference between their results.

Transfer

Ten attempts were made to carry out the complete parasitic stage on the original host medusa and two were successful. Eight attempts failed owing to death or diseased condition of the host medusae after a long period in culture. In the successful attempts the host medusa were in very poor condition and unable to swim off the bottom at the time the anemones burrowed into the sand. A larval anemone 2 mm in length is able to eat all four gonads off a host in two days. It will then generally proceed to eat the manubrium, stomach and tentacles and, in a few cases, the mesoglea of the bell itself. If given the opportunity under laboratory conditions the parasitic anemone may transfer from one medusa to another.

Numerous transfers have been observed in the laboratory and a few were photographed using a 16 mm motion picture camera. The transfer process involves three stages. (1) Contact between the parasitic anemone and a potential host medusa (Fig. 3a). (2) A period of adherence by nematocysts to both the new potential host and the old original host medusa (Fig. 3b). (3) Release of the original host (Fig. 3c). The complete transfer process from initial contact to release of the old host may take as little as 10 seconds or may last for more than an hour. During a transfer, the anemone is able to hold two actively swimming medusae in spite of very small contact areas (Fig. 3d). In the growth experiments a new medusa was put into the culture dish when it was observed that the old host lacked three or more gonads. After the transfer the old host was removed. In the 1970 experiment the anemones ate an average of 14.6 gonads, involving an average of three transfers. The transfers are possible at all times during the ectoparasitic phase, but are more likely to occur during the early or middle part of the phase. Large parasites (4 to 5 mm in length) show less

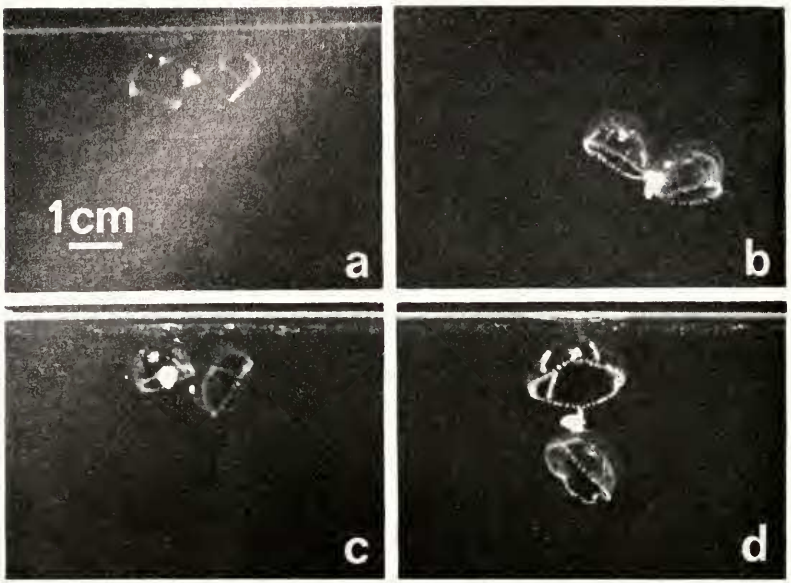

FIGURE 3. Photographs from a 16 mm motion picture record of the transfer by *Peachia quinquecapitata* from one host to another. (a) Two medusae touching so that the parasitic anemone, attached to the medusa on the left, makes contact and adheres to the other medusa; (b) the parasite firmly attached to the two medusae; (c) the parasite just after completing the transfer. The previous host medusa is on the right and the new host is swimming away to the left; (d) a parasite holding a medusa with the tip of one tentacle. The body of the anemone is attached to the original host. Both medusae were swimming during this sequence and the transfer was successful.

tendency to adhere to a new medusa when contact is made and will often remain on their "final" host for a week.

Dip net collections of medusae made in 1967 indicated that the female specimens of *Phialidium* were more heavily parasitized than the males. The hypothesis that the parasite would transfer more readily to a female medusa than a male was tested in a series of 382 tests. In these tests a pair of male and female medusae were placed in the culture jar with a parasite whose host had three or more gonads missing. The pair were chosen to be similar in size and activity on the assumption that the probability of contacting the parasite would be the same. The culture was examined the next day and the sex of the new host noted. Of the 117 successful transfers, 58 were to females and 59 to males. A Chi square value of 0.002 indicates no preference for either sex in transfer. A rank correlation test was run on the 1967 growth data comparing the length of the ectoparasitic phase and proportion of female to male gonads eaten by the parasites. The rank correlation test showed a strong correlation and suggested that those parasites that ate a larger proportion of female gonads in comparison to male gonads became free-living more quickly. Accordingly, in the 1970 study each parasite was restricted to hosts of the same sex as its original host. Thirty such tests were started, fifteen each of males and females. Those restricted to males took an

average of 41.2 days for the ectoparasitic phase, ate an average of 15.2 gonads, and were on the average 4.6 mm long when they became free-living. Those restricted to female hosts were ectoparasitic an average of 39.75 days, ate an average of 13.6 gonads, and were on the average 3.7 mm long when they became free-living. Six males and four females survived to the free-living stage. The *t* test applied to these means shows no significant difference between the anemones raised on male or female hosts.

Once off the final host, the anemones burrow quickly into the sand in the manner described by Ansell and Trueman (1968). The average size of all ten animals at the termination of the parasitic stage was 4.19 mm long, 2.25 mm in diameter and with 0.74 mm tentacles. These animals are still being maintained in a sea water table with the adults.

Incidence of parasitism

Records were kept of the percentage of the host medusae, *Phialidium gregarium,* that were parasitized in each dip net collection. The collections made in 1967 showed 8.9% parasitism for the week starting 18 June. The incidence of parasitism increased to 14.1% in the week starting 10 July and declined to a low of 5.0% during the week starting 13 August (the final week of collections). In 1970, collections made on 17 and 19 May contained no parasitized medusae. A collection taken on 2 June had 13.3% parastized medusae. Subsequent collections during June 1970 showed 33.3 to 62.5% parasitized medusae, many of which had endoparasities. Owing to my greater familiarity with the endoparasitic phase, these 1970 records are probably more accurate than those of 1967.

In addition to *Phialidium gregarium* the medusae *P. hemisphaericum, Aequorea aequorea, Halistaura cellularia* and *Mitrocomella polydiodemata* are sometimes parasitized in the Friday Harbor area.

Discussion

The morphology of the anemone used in this life cycle study conforms to the description given by McMurrich (1913) in all but one detail. McMurrich stated that although the central area of the physa in his specimens was very thin, he saw no perforations. Other members of the genus have rows of cinclides on the physa between the insertions of the septa (Carlgren, 1949). During my study, I observed rows of cinclides on the physa of *Peachia quinquecapitata,* in both the free-living adults and the large parasites 5 mm or longer in length. In order that they be visible, the anemone must be very well expanded and propertly illuminated. McMurrich described preserved specimens which were probably not expanded well enough to show the cinclides.

The description of spawning by *Halcampa duodecimcirrata* (Halcampidae) (Nyholm, 1949) is similar to that observed in *P. quinquecapitata.* The major difference is the degree of extension from the burrow. Whereas *H. duodecimcirrata* extends the entire length of its scapus out of the burrow, *P. quinquecapitata* rarely extends more than one-half of the scapus. The data from the laboratory spawnings of *P. quinquecapitata* indicate that most commonly the males begin to release gametes first and that this may stimulate the female to release eggs. This

is in general agreement with the observations of Nyholm (1949), but these data should not be taken as conclusive evidence of female stimulation by the male without further experimentation.

The spines of the egg of *Peachia* were first described by Faurot (1895). He felt them to be formed of "vitelline" membrane. The eggs of *Tealia crassicornis* (*Urticina*) are covered by spines (Appellof, 1900), as are the eggs of *Actinia* and *Bolocera* (Gemmill, 1920). Preliminary observations using the electron microscope indicate no extra membranes on the unfertilized egg of *P. quinquecapitata* and no changes have been observed after fertilization viewed with light optics. The function of these spines is not apparent. The eggs of *P. quinquecapitata* are negatively buoyant so their function is not flotation. The spines would function in attachment to the host medusae. However, my observations indicate that by the time the cilia are developed and the larva is swimming, the spines are reduced or have disappeared completely. The pre-swimming stage is short in relation to the planktonic stage (20 hours *vs.* 30 days under laboratory conditions), so that the probability of this being the time of host-parasite interaction is small. In addition I have shown that the initiation of the parasitism takes place readily during the planula phase.

Observations that the medusa of *P. gregarium* feeds upon the planula do not rule out host-seeking behavior on the part of the planulae. In the few experiments made to test for such behavior, none could be found. More elaborate experiments might reveal such behavior, but host-seeking is not a prerequisite to the initiation of parasitism. The tendency of the planulae to seek light would put them into regions where they might be fed upon by the medusae.

During the endoparasitic phase, the anemone is subject to conditions within the gastrovascular cavity of the host. The observation that the larvae would begin to develop in a medusa fed on natural plankton, but not in a starved medusa or one fed on *Artemia* indicates that some specific conditions may be necessary to initiate development. The results of the 1967 experiments, in which the larvae had already begun to develop before brine shrimp were fed to the medusae, argue that once development begins, conditions in the host may be less critical to the parasite.

During the endoparasitic phase the larval anemone appears to derive its nutrition from the partially digested material in the host gastrovascular cavity. The larvae are usually found in the area of the radial canal under the gonad. It is known that partially digested material circulates in the gonadal part of the radial canal (Roosen-Runge, 1967). In addition to food uptake by the gastrodermis of the parasitic anemone, sectioned material shows the epidermis to have characteristics of a phagocytic epithelium. This epithelium changes character during the different phases of the anemone's life cycle, which indicates a change in its function.

Faurot (1895) reported that larvae of *Peachia* obtained from fertilized eggs and cultured in the laboratory died two days after fertilization (probably at the planula stage). I was able to keep planulae alive for up to 30 days after fertilization, but with no evidence of growth or development. Planulae which were put into a host medusa began to grow and differentiate within one or two days. This indicates that a period of time in the gastrovascular system of a medusa may be necessary for the initiation of development. Such situations are not uncommon in gut parasites such as nematodes which have been shown to need specific stimulae to trigger

hatching or development (Rogers, 1960). The fact that *Peachia* planulae did not grow or differentiate in my cultures is not proof of an obligate parasitism, but it argues strongly in favor of this hypothesis.

During the ectoparasitic phase, the larvae of *P. quinquecapitata* feed on the gonads and other body tissues of the host medusa. Earlier authors have reported different observations on other species of *Peachia*. In most cases the term parasite has been used in a very general sense. Müller (1860, page 435) reported that the parasitic anemones he had collected contained "fragments of tentacles, filaments, genitalia, stomachal filaments, etc." in their gastrovascular cavities. However, he noted that the parasites could go for months without food and would eat things other than medusae. Haddon (1887) fed the parasites small pieces of meat when no medusae were available. He stated that the medusa was probably killed by the parasite, but gave no evidence for this. I have maintained a few larvae of *P. quinquecepitata* on shrimp and clam meat, but none ever completed development to the adult stage. McIntosh (1887) stated that it was not necessary to limit the parasite to feeding on medusae. He suggested that the anemone could capture food with its mouth while remaining attached to the medusa with tentacles. This type of behavior was not observed in my study of *P. quinquecapitata*. Browne (1896) described *Peachia* on the gonads of the hydromedusa *Phialidium*, but did not report whether they were feeding on the gonads.

Badham (1917) describes the tubular siphonoglyph and conchula as larval structures functional in feeding. He describes a constant stream of water passing into the conchula and out through the physal cinclides of parasites 5 to 40 mm in length. It should be pointed out that the species which he studied (*P. hilli*) was living inside the radial canals of a large rhizostome medusa, *Crambessa mossica*. Panikkar (1938) describes a stream of water passing into the conchula of *Metapeachia tropica* (*P. tropica*) attached to the subumbrellar surface of *Aequorea pensile*. He noted that until the conchula and siphonoglyph were developed, no food was seen in the gastrovascular cavity. After these structures developed, diatoms and copepods were always found in the gastrovascular cavity of the parasite. I have observed pores in the physa of parasites over 5 mm in length, and although a stream of water was observed to pass into the siphonoglyph in a few cases, no particles were seen to pass into the anemone. This was not observed in smaller anemones and many became free-living before the pores become noticeably differentiated. It is possible that *P. quinquecapitata* supplements its diet of gonad with food carried in by ciliary currents, but I have not observed it.

Transfer behavior has not been described for *Peachia* before, Ross (1967) has described the transfer behavior of the anemones *Calliactis, Stomphia, Actinostola* and others toward mollusc shells with which they are associated. These transfers involve initial sensing of the shell by the anemone through tentacle contacts. This is followed by adhesion of the tentacles through nematocyst discharge and a detachment of the base of the anemone. Movements then bring it into contact with the shell to which the tentacles are attached and the tentacles are released. The transfer of *P. quinquecapitata* does not involve the active movement of the anemone from one host to another but does involve recognition and attachment by the discharge of nematocysts and adherence to the new host. This is followed by a differential release of nematocysts which results in the release of the old host and

continued adhesion to the new host. The actual separation from the old host is accomplished through the swimming of the medusae and not movement of the larva.

This transfer has not been observed in nature, but it reasoned to occur there. Most medusae collected with a parasite are missing one or more gonads. Occasionally a medusa is collected bearing a parasite 2 mm or longer, but still having all four gonads intact. It is presumed that in these cases transfer had recently occurred. In cases where such infected medusae were kept in the laboratory the parasites began to eat the gonads within a very short time.

It has been demonstrated that a parasite can develop to the free-living stage on the original host and that transfer is not necessary. The hosts in these cases were essentially dead at the end of the parasitism. Transfer to a new host would provide better nutrition and transportation for the parasite and preserve the life of the host. It has been shown by Roosen-Runge (1965) that the medusa *Phialidium* can regenerate gonads within 14 days after their surgical removal.

Phialidium gregarium occurs in dense swarms in the Friday Harbor area and although no quantitative measurements have been made to determine densities, I have observed contacts between medusa. I hypothesize that contacts occur frequently enough to permit transfers of the larvae.

Contrary to Nyholm (1949), I conclude that *P. quinquecapitata* is an obligate parasite for at least a short period during its development. The apparent inability of the free-living planula to continue development, the specialized feeding behavior as an ectoparasite, and the transfer behavior are adaptations which seem well suited to a period of parasitic life. Other species in this genus may not parasitize their hosts in the same way as *P. quinquecapitata* or may not be obligate parasites. Answers to these questions await more detailed studies of the other species.

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Summary

1. *Peachia quinquecapitata* kept in sea water tanks at the Friday Harbor Laboratories were induced to spawn. The egg is 120 μ in diameter and is covered with spines 20 μ in length.

2. Cleavage leads to a hollow blastula which becomes ciliated. As the cilia appear the spines become shorter and disappear.

3. Gastrulation is by invagination. The planula stage is reached when the gastrula develops an apical tuft of long cilia.

4. A swimming planula can be ingested by the medusa *Phialidium gregarium*. After ingestion the larva begins to grow and differentiate. Planulae which did not get ingested would not develop in the laboratory.

5. The larvae remained endoparasitic for an average of 11 days and probably were feeding on material in the gatrovascular cavity of the host medusa.

6. After 11 days the larvae became ectoparasitic and fed on the gonads of the host medusa. After an average of 31 days of ectoparasitism anemones had acquired their adult characteristics and dropped off the host medusa to become free-living.

7. During the ectoparasitic phase the larval anemones could transfer from one host medusa to another in the laboratory cultures. Transfer has not been observed in nature but is reasoned to occur there.

LITERATURE CITED

Agassiz, L., 1859. On some new actinoid polyps of the United States. *Proc. Boston Soc. Natur. Hist.*, **7**: 23–24.

Ansell, A. D., and E. R. Trueman, 1968. The mechanism of burrowing in the anemone, *Peachia hastata* Gosse. *J. Exp. Mar. Biol. Ecol.*, **2**: 124–134.

Appellof, A., 1900. Studien uber Actinien-Entwicklung. *Bergens Museums Aarbog*, No. 1, 3–99.

Badham, C., 1917. On a larval actinian parasitic in a rhizostome. *Quart. J. Microscop. Sci.*, **62**: 221–229.

Browne, E. T., 1896. On British hydroids and medusae. *Proc. Zool. Soc. London*, **1891**: 459–500.

Carlgren, O., 1949. A survey of the Ptychodactaria, Corallimorpharia and Actiniaria. *Kongliga Svenska Vetenskademiens Handlingar, Fjarde Serien*, **1**: 1–121.

Faurot, L., 1895. Etudes sur l'anatomie, l'histologie, et le developpement des actinies. *Arch. Zool. Exp. Gen.*, **3**: 43–262.

Gemmill, J. F., 1920. The development of the sea-anemones *Metridium dianthus* (Ellis) and *Adamsia palliata* (Bohad). *Phil. Trans. Roy. Soc. London, Series B.*, **209**: 352–375.

Haddon, A. C., 1887. A note on the arrangement of the mesenteries in the parasitic larva of *Halcampa chrysanthellum*. *Sci. Proc. Roy. Dublin Soc.*, **5**: 473–481.

McIntosh, N. C., 1887. Notes from the St. Andrews Marine Laboratory, 3. On the commensalistic habits of the larval forms of *Peachia*. *Ann. Mag. Natur. Hist.*, Series 5, **20**: 97–104.

McMurrich, J. P., 1913. On two new actinians from the coast of British Columbia. *Proc. Zool. Soc. London*, **1913**: 963–972.

Müller, F., 1860. On *Philomedusae vogtii*, a parasite on medusae. *Ann. Mag. Natur. Hist.*, Series 3, **6**: 432–436.

Nyholm, K. G., 1949. On the development and dispersal of Athenaria with special reference to *Halcampa duodecimcirrata*, M. Sars. *Zool. Bidrag Fran Uppsala*, **27**: 465–505.

Panikkar, N. K., 1938. Studies on *Peachia* from Madras. *Proc. Indian Acad. Sci., Section B*, **7**: 182–205.

Rodgers, W. P., 1960. The physiology of infective processes of nematode parasites; the stimulus from the animal host. *Proc. Roy. Soc. Series B*, **152**: 367–386.

Roosen-Runge, E. C., 1965. Regeneration of gonads in *Phialidium* (Hydromedusae). *VIII International Congress of Anatomists*, **1965**: 101.

Roosen-Runge, E. C., 1967. Gastrovascular system of small hydromedusae: mechanisms of circulation. *Science*, **156**: 74–76.

Ross, D. M., 1967. Behavioral and ecological relationships between sea anemones and other invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.*, **5**: 291–316.